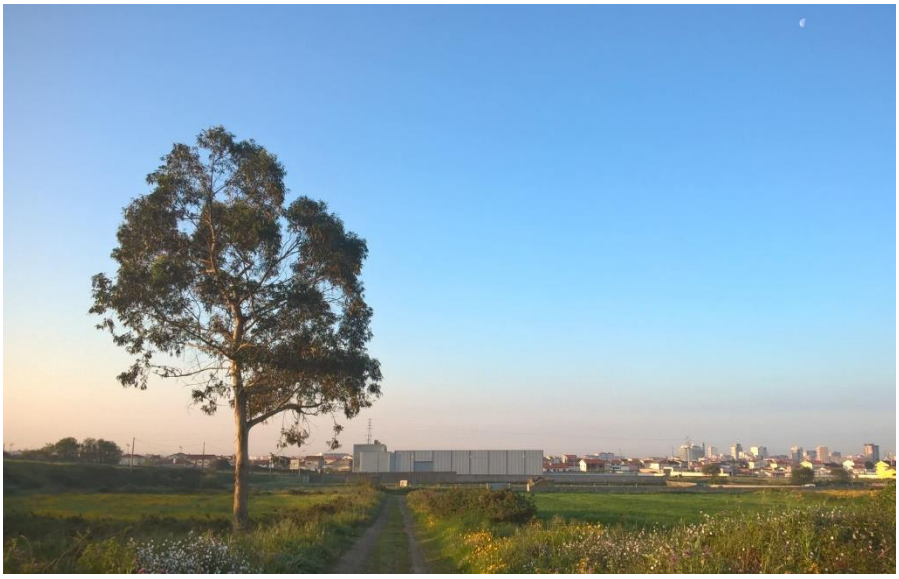

Exotic-Exotic and Exotic-Native interactions during the invasion of Common Waxbills in Iberia

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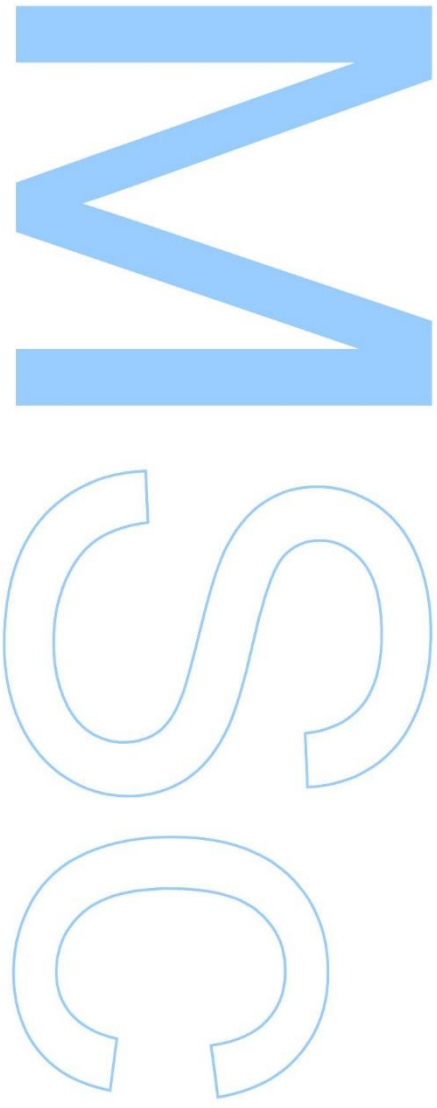

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Al'lalum!!!

Abstract

Biological invasions are an important and very debated topic in ecology. The known impacts they can have on human society and ecosystems alike have been a cause of concern for many decades.

However, although invasive species are considered to have mostly negative effects on ecosystems (e.g. interspecific competition), the possible neutral or even positive interactions with native and other exotic species are often overlooked. For example, the occupation of vacant niches or the use of unexploited resources may have neutral or even beneficial effects on ecosystems.

A Portuguese agricultural system invaded by the common waxbill (*Estrilda astrild*), a small granivorous bird, and several exotic plant species was chosen to assess the potential for competition for food with a native granivorous bird and to test for an influence of exotic plant species in that competition. The chosen location exhibits several heterogeneous agricultural parcels, which makes grants it representativeness and allows sampling of preferences of birds on several plant species.

The common waxbill's food preferences were compared with the granivorous native species', European serin (*Serinus serinus*), to measure their overlap. The similarities to common waxbills in habitat (agricultural fields) and morphology (size and weight) made the serin the best native species for these tests.

Food preferences of both common waxbills and European serins include, according to observations, exotic plant species. A clear preference for different plant species and a very low overlap in their feeding habits, especially during the most critical season of the year (winter time), reveals a low potential for food resource competition and an ecologically differentiated feeding niche. Allied to the fact that the common waxbills in this area fed mainly on exotic plant species during a season of less stressful environmental and physical conditions (autumn time), a suggestion towards facilitative exotic-exotic interactions during the invasion of common waxbills is plausible. The facilitation exotic plant species may provide to common waxbills comes in the form of food resource availability and alleviation of the potential competition with native birds.

Keywords

Invasion ecology; Common waxbill; Exotic species; Competition; Facilitation; Vacant niches

Sinopse

As invasões biológicas são um tópico da ecologia extremamente debatido e importante. Os impactos conhecidos que estas podem ter na sociedade humana e em ecossistemas têm causado preocupação na área nas últimas décadas.

Contudo, apesar de ser considerado característico das espécies invasoras causar, maioritariamente, efeitos negativos nos ecossistemas (e.g., competição interespecífica), as possíveis interações neutrais ou positivas com espécies nativas ou outras espécies exóticas são, muitas vezes, ignoradas. Por exemplo, a ocupação de nichos vazios e o uso de recursos não explorados podem ter efeitos neutrais, ou até benéficos, em ecossistemas.

Um sistema agrícola em Portugal invadido pelo bico-de-lacre (*Estrilda astrild*), um pequeno pássaro granívoro, e muitas espécies exóticas de plantas foi escolhido para determinar o potencial de competição por recursos alimentares com uma ave granívora nativa e para testar a influência de plantas exóticas nessa competição. A localização escolhida apresenta diversas parcelas agrícolas heterogéneas, o que lhe confere representatividade e permite amostrar eventos de preferências de aves em diversas espécies de plantas.

As preferências alimentares do bico-de-lacre foram comparadas com as da espécie granívora nativa, o serino europeu (*Serinus serinus*), para medir a sua sobreposição. As semelhanças morfológicas (peso e tamanho) e de habitat (campos agrícolas) partilhadas entre o bico-de-lacre e o serino tornam o serino a melhor espécie nativa para o que se pretende testar.

De acordo com as observações efetuadas, as preferências alimentares do bico-de-lacre e do serino incluem plantas exóticas. A clara preferência alimentar por determinadas espécies e a pequena sobreposição nos eventos de alimentação, especialmente durante a época mais crucial para a sobrevivência (época invernal), revela um baixo potencial para competição interespecífica e um nicho ocupado pelo bico-de-lacre que é ecologicamente diferenciado do do serino. Aliado ao facto de que os bicos-de-lacre se alimentaram, na grande maioria, de plantas exóticas durante a época de menor stress físico e ambiental (época outonal), há uma sugestão que aponta para que haja interações exótico-exótico facilitadoras durante a invasão biológica do bico-de-lacre. Esta possível facilitação que as plantas exóticas poderão

fornecer ao bico-de-lacre aparece sob a forma de disponibilidade de recursos alimentares e da redução do potencial para competição com espécies nativas granívoras.

Palavras-chave

Ecologia das invasões; Bico-de-lacre; Espécies exóticas; Competição; Facilitação; Nichos vazios

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List of Abbreviations

GHC - General Habitat Categories

MPH - Medium Phanerophytes Evergreen

QGIS – Quantum Geographic Information System

GMT – Greenwich Mean Time

AM – *Ante meridiem* (before noon)

AA – Autumn Area

WA – Winter Area

1. Introduction

1.1. Biological invasions' context

Humans have, since the beginning of the era of agriculture and domesticated animals, transported species for feeding purposes, like cuscus (*Phalanger orientalis*) and the flightless rail (*Nesotrichis debooyi*), during their migrations (Grayson, 2001). The history of biological invasions, (i.e. of species that were transported out of their native range by humans and expanded autonomously in new habitats where the native species were unused to its presence), starts with this first documented act of transportation of the cuscus and the flightless rail by human hands (Blackburn et al., 2009). This act of translocating species has had enormous impacts into how humans developed and live nowadays, has been happening for millennia (Hulme, 2009) and has led to a definition of what is now a very well-studied and immensely debated subject, the science and research of biological invasions.

Biological invasions are widely studied across the world because of the deep impacts that transported species can have in ecosystems, economy and our daily lives. Even though this is a subject that affects many countries, there are a few countries whose available resources and extreme situations of invasion have led to higher efforts and dedication into this research. America, Europe and Australia are the continents that have produced most of the information regarding this subject (Blackburn et al., 2009; Evans et al., 2014; Martin-Albarracin et al., 2015; Evans et al., 2016), while New Zealand and Hawaii have received very special attention as well because of how they are a basin of exotic species and because of the deep impacts these species can have on island ecosystems and native species (Blackburn et al., 2009). In Europe alone, a highlighted increase in the annual rate of introductions started during the Industrial Revolution Era (1800 AD) because of the constructions of railroads and highways (Findlay & O'Rourke 2007) and because of human emigration from Europe (McNeeley, 2006). The highest rates of introduction, however, have happened during the last 25 years because of the effects of globalization (Hulme, 2009), such as the easy access to other countries and the spread of animal sales related to trends or cultural reasons. A very recent example of this is the increase in the sales of the common clown fish (*Amphiprion ocellaris*) and of the Indo-Pacific surgeonfish (*Paracanthurus hepatus*) after the movies "Finding Nemo" and "Finding Dory" came out in 2003 and 2016, respectively (Garrard, 2010; Maison & Graham 2016). The exponential increase in the

frequency of invasions gave this subject the much needed attention it deserves (Bauer & Woog 2011), in order for scientists that study biological invasions to better understand the biology behind this phenomenon and to determine in which cases prevention and management of invasive species is possible and necessary.

One of the major issues regarding biological invasions starts with the definition of the invader. The nomenclature that is used to define a species that has been inserted into a new territory has followed many trends and, depending on the study, different descriptions can be used in order to better demonstrate the objectives of the study and how the species influence the tested environments. The definition of exotic species used by many authors (Duncan et al., 2003; Falk-Petersen et al., 2006; Blackburn et al., 2009; Baker et al., 2014; Batalha et al., 2013; Stiels et al. 2015) is that of species that were transported out of their historical range by humans. The literature diverges in this definition. Concepts regarding the terms “alien” and “invasive” often include the negative impacts on ecosystems and species, such as hybridization and disease transmission, and on human society, through economical losses. Thus, I decided to join a more seemingly neutral nomenclature: exotic species (Pereyra, 2016), instead of the invasive species terms and its synonyms. Despite its simplicity, I decided to adopt this definition in order to stray from the immediately assumed impacts exotic species may eventually have on ecosystems. There are other neutral nomenclatures, such as “non-native” (Bauer & Woog 2011; Pereyra, 2016), but the term “invasive” is often imbued in a negative connotation, seeing as they are immediately assumed to have negative impacts on human economy and resources, and in other species or environments (Falk-Petersen et al., 2006; Ricciardi & Cohen 2006; Blackburn et al., 2009). “Invasive” species are described as species transported outside their natural range and that have established successfully, but with the added negative impacts they might bring to these newly invaded environs (Pyšek et al., 2007). This conceptual grasp of negative impacts from exotic species is appropriate and should be considered in the study of biological invasions (Bruno et al., 2003; Goodenough, 2010), as many species and environments, especially in islands, suffer greatly from uncontrolled introductions. Exploring how this might not always be the case is, however, necessary and lacking.

1.2. Exotic species – definition controversy and impact typing

It becomes clear that exotic species are one very important variable that can sway the ecological equilibrium of Earth’s environs because of the great impact they can have on

them. More specifically, exotic bird species are known to affect global biodiversity, human health and human commensalism (Simberloff et al., 2013; Martin-Albarracin et al., 2015) because they give rise to new pressures that the native species did not have to deal with before (Whittaker & Fernández-Palacios 2007), such as predation, competition, parasitism, hybridization, disease transmission and interaction with other exotic species (Blackburn et al., 2009; Goodenough, 2010; Stiels et al., 2015; Tassin & Kull 2015; Martin-Albarracin et al., 2015; Evans et al., 2016).

The most supported view of invasion ecology, and the one that gave rise to modern invasion science in the mid-1980's (Simberloff, 2010), is one that sees exotic species as having negative ecological impacts on ecosystems and their native species (Bruno et al., 2003; Duncan et al., 2003; Schlaepfer et al., 2011; Tassin & Kull 2015; Gilroy et al., 2016, Pereyra, 2016). This negative mindset regarding exotic species originates from studies that focus on what is foreseen as the negative aspects of invasive species (e.g. interspecific competition; Simberloff & Von Holle 1999; Bruno et al., 2003; Sol et al., 2011; Martin-Albarracin et al., 2015). Not only is this view highly influenced by human social and ethical context (Tassin & Kull 2015), but it is also considered erroneous by many authors for research to follow this path alone (Richardson et al., 2000; Ricciardi & Cohen 2006; Goodenough, 2010; Schlaepfer et al., 2011; Baker et al., 2014; Pereyra, 2016), as this focus on negative impacts creates a bias in the way research is conducted and expresses but one part of the whole array of possible interactions (Tassin & Kull 2015). Hence, it is necessary to include in research the idea that not all invasive species will, mandatorily, affect ecosystems negatively, rather, there might be positive interactions that are present but unidentified. Again, the idea of negative impacts is not to be overlooked by studies, as it is important to determine these impacts and how they affect the environments in which the introductions occur. However, there is a need for a paradigm shift in the established notion of negativity that hovers around the "invasive" or "alien" terms (Richardson et al., 2000; Simberloff et al., 2013) and for a more holistic view of biological invasions in order to go beyond the established prejudices (Tassin & Kull 2015).

Many studies (e.g., Richardson et al., 2000; Goodenough, 2010; Baker et al., 2014; Martin-Albarracin et al., 2015) have fought the established notion that exotic species are ecologically detrimental and, instead, consider these impacts as a very complex and branched system of interactions which may be positive, negative or a mix of both effects. Research can be affected by the position an author takes regarding exotic species (Simberloff et al., 2013), because if an author considers these species as

detrimental, *a priori*, then the experimental design may focus on discovering these negative impacts, which, in turn, creates a research bias.

Mutualisms, ecosystem services (e.g. pollination, seed dispersion), predation, competition, functional diversity and many others can have unexpected effects on ecosystems (Simberloff et al., 2013), which may be hard to define as fundamentally positive or negative. It is also useful to understand that an interaction may not be either positive or negative forever, which is due to the fact that ecosystems suffer from cumulative effects (Eherenfeld, 2011) and have intricate relationships (Duffy et al., 2007) that are not entirely predictable and that can result in observations of both extremes, depending on the timing in which the studies are made. Some interactions may prove to be negative in a short-term time frame, but neutral or even beneficial in the long-term (Goodenough, 2010), something that is rarely taken into account whenever a study focuses on negative impacts, as happened with the red imported fire ants (*Solenopsis invicta*), which caused a dramatic reduction in population size of native arthropods (Porter & Savignano 1990) during their introduction in Texas, USA. A repeat study 12 years later (Morrison, 2002) showed that the same native populations recovered their original sizes. The relationships and changes associated with invasions can never be completely accounted for in one immediate study (Ricciardi & Cohen 2006), as this study will represent but a fragment of time and can lead to misinterpretation of the long-term effects the new species had on the ecosystem and the native species that inhabited it.

1.3. Arrival at new ecosystems and related consequences

One of the ways in which exotic species may enter a habitat with no negative consequences for the native species is through the exploration of vacant niches or unexploited resources (Tilman, 2004; Sol et al., 2012; Batalha et al., 2013; Sullivan et al., 2015; O'Loughlin & Green 2015). Anthropogenic changes to natural habitats (e.g., agricultural sites or rice fields) are, often, the precursors to new resources (Sax & Brown, 2000; Sol et al., 2011) and allow for the continuous existence of food supplies (Shochat et al., 2006) and for the creation of opportunistic situations for exotic species to establish (Case, 1996). The opportunities arise for exotic species because, for example, the functional diversity of the native species (such as morphology, explorative behavior and interspecific relationships) that occupied that habitat may not react to all the fast changes imposed on the ecosystem by human alteration (Shea & Chesson 2002; Sol, 2016). This may leave gaps in usable resources that could be filled by exotic

species (Sullivan et al., 2015), because natives may not utilize them to their full potential (i.e., an underexploited resource that results in a vacant ecological niche). An example of underexploited resources is found in urban environments, where exotic birds rely, mostly, on food provided by humans (Sol et al., 2012)). Unexploited resources and vacant niches increase community invasibility by creating ecological opportunities for exotic species (Tilman, 2004; Sullivan et al., 2015). This action taken by exotics does not require that there will be negative changes in the biodiversity that was previously present, as communities can often accept additional species (Stohlgren et al., 2008) without competition for resources (Bulleri et al., 2008), rather, coexistence is likely, seeing as these resources were unused by native species (Goodenough, 2010; e.g., exotic and native bird species coexist due to the exploration of vacant temporal niches related to breeding season (Sanz-Aguillar et al., 2015)).

Some exotic species may, therefore, occupy a position in the ecosystems that they are introduced in which does not, necessarily, negatively affect the species that were part of it prior to their arrival (Bulleri et al., 2008). One of the ways in which exotics may do so is, as is mentioned above, by exploiting new resources that become (or were) available and may be derived from human action. This exploitation may also be seen as a facilitator of invasion, in tandem with positive species interactions, because it grants new species the opportunity to join the community. Facilitation in invasion biology is represented by any interaction that is beneficial to one of the parties and affects none of them in a negative way (Bruno et al., 2003; Simberloff, D. 2006; Bulleri et al., 2008). This concept can take many forms, such as mutualisms, novel or already existent resources unexploited by natives, vacant niches and whatever other consequences related to interactions between species that may increase the chances of an ecosystem accepting new residents (Richardson et al., 2000; Bruno et al., 2003). The field of facilitation between species, especially between exotic species, has received an increase in attention because it is a mechanism that increases communities' invasibility (Mitchell et al., 2006; Saccone et al., 2010). Exotic species may interact with other exotics or with native species and, in those interactions, benefit both or the other without receiving any reduction in their fitness. There are several ways in which such interactions between both fauna and flora may increase how easy it is for a community to accept new members. Some examples include facilitation through shading, protection from herbivory or grazing, increase in available food resources, removal of predators or deterring predators, reducing thermal/water/nutrient stress, mutualisms (e.g. seed dispersers), diversification/enhancement/replacement of

food sources, aid in translocation (from species endangered in their own native ranges: “assisted colonization” (Hoegh-Guldberg et al., 2008)) and many others that reflect the complexity of the communities in which exotic species are introduced (Bruno et al., 2003; Bulleri et al., 2008; Tassi & Kull 2015; Chupp & Battaglia 2016).

In this thesis, exotic-native and exotic-exotic interactions shall be explored in order to shed some light into the invasion of the exotic bird species, the common waxbill (*Estrilda astrild*). Studying these interactions by comparison with an ecologically similar native species, the European serin (*Serinus serinus*) will add to the understanding of how the common waxbill has been affected and affect other species in the studied area.

1.4. Model species

The exotic species used in this thesis was the common waxbill, a very successful invasive species in many parts of the world (Stiels et al., 2011). It is a seed-eating bird (mostly Poacea seeds; Batalha et al., 2013; Stiels et al., 2011; Sanz-Aguillar et al., 2015), originally from the sub-Saharan Africa, that has become a very widespread and successful species in the southwestern part of Europe, namely, the Iberian Peninsula. In Portugal, where there is suitable habitat, and in adjacent parts of Spain (Reino, 2005; Reino & Silva 2009; Sullivan et al., 2012), the common waxbill can be found as the lightest bird out of all the native seed-eating birds (Sullivan et al., 2015) and as one species that travels and feeds in groups (pers. obs.; Stiels et al., 2011). In Iberia, common waxbills inhabit mainly human modified areas (i.e. agricultural areas; Stiels et al., 2011) that have some sort of riparian vegetation, which they use for roosting, shelter and nesting. The native species that is most similar in terms of feeding, size and weight is the serin, which also occupies human modified areas and feeds off of seeds (Diaz, 1990). Both the waxbill and the serin inhabit the study area, which also contains exotic and native plant species associated with agricultural fields and disturbed habitats.

A previous study concluded that common waxbills most likely occupied a marginal ecological niche (either vacant or highly differentiated) relative to the community of native passerines in Portugal (Batalha et al., 2013). Batalha et al. (2013) compared ecological traits of sympatric native passerine species and the common waxbill, so as to estimate niche distances (used as a proxy of niche dissimilarity) and infer potential competition between the species, since niche similarity is considered to be an indicator of the potential for interspecific competition (Schoener, 1982). If native communities are

saturated and in equilibrium, exotic species must overlap with the niche space of some native species and compete for resources. If, however, native communities are not saturated and have, therefore, vacant or unexplored ecological niches, then some exotic species may take advantage of unused resources. The occupation of vacant or unexplored niches by an exotic species is not, necessarily, detrimental for native communities. Ecological distances between common waxbills and native species in Portugal were found to be identical or larger when compared with the ecological distances among the native species' community. This suggests that common waxbills entered an unsaturated ecosystem on which it occupies a differentiated ecological niche (Batalha et al., 2013). To deepen the knowledge on common waxbills' occupation of a vacant niche, ecological traits must be looked at in more detail, rather than through a sum of many that characterize the occupation of a niche. To do so, ecological traits, such as feeding habits and preferences, may be divided and individually analyzed, whilst still using native models as comparison.

1.5. The thesis' goals

The main objective of this thesis is to search for understanding on whether the occupation of what is believed to be a vacant niche by common waxbills (Batalha et al., 2013) led to competitive interaction with a specifically chosen native species, and to understand whether there is facilitation from exotic plant species, abundantly present in the study area, in the ongoing establishment of this exotic bird species. I use a native species, the European serin, as a model for comparison and to test for interactions.

To do so, firstly, observations were made to test for food preferences of both species, which would reveal both the diet of the bird species and whether the feeding was proportional to the plants' abundance in the study area or not. Secondly, an overlap was looked for in the feeding events to see how it varied in the observed seasons (serotinal/autumnal and wintry/prevernal). Determining whether there was potential for competitive behaviour in the most crucial season for potential competition for resources through overlap in feeding habits may indicate if there are negative serious ecological consequences associated to this exotic species. The most crucial season, the wintry/prevernal season, had the harshest weather and a scarcity of previously abundant food resources. Lastly, the alleviation (through exotic plant species) in the overlap of the food preferences was tested by investigating the changes that exotic plant species would create when removed from the overlap calculations. Testing for

this alleviation by exotic plant species allows for the discussion of potential facilitative interactions.

With this thesis, the suggestion of the vacant niche occupation by Batalha et al. (2013) will be explored, the food preferences of both species will be determined, the potential competition with a native species will be tested and the potential facilitation from exotic plant species will be assessed.

2. Methods

2.1. Study area and feeding observations

Location and land use

Observations of common waxbills and serins foraging in an agricultural site were conducted in the northwestern part of Portugal, near Póvoa de Varzim. The study site was characterized by small, highly irrigated agricultural plots, which varied in the crops planted, with seasonal variation in those crops. These included various horticultures (onions, cabbages, carrots, and others), corn fields, and also fallow plots during part of the year or year-round. The non-planted flora of the site was mostly composed of bushes and small plants, found amongst the cultivated plants and along the borders of agricultural plots, paths and fallow fields. The study site was chosen because of its spatial and temporal heterogeneity in agricultural use, which makes it representative of the traditional agricultural land use in this region, and because common waxbills and serins can be observed year-round at this site (personal observation). Previous studies show that both waxbills and serins inhabit farmland, amongst other sorts of habitats, and that open farmland is their main foraging habitat (Reino & Silva 1998; Svensson et al., 2010).

Observations: area, seasons and procedure

Observations were made on a corridor of ca. 60 meters wide, 30 meters to each side of a dirt road that circles around the field site, for 710 meters in length (Figure 1). The 30-meter distance on each side was chosen because it allowed for the detection of birds and a clear observation of them feeding, with the use of binoculars. Some slight adjustments to this 30-meter distance had to be made because of physical barriers present in the fields. The observation area was 3.7 ha. Observations were conducted from 7 to 11AM, which encompasses the morning period of highest feeding activity, during two field seasons (Table S1). Observations were not made on days of intense or

continuous rain and/or strong winds, which contributed to the field seasons having different durations. The first field season corresponds to the serotinal and autumnal vegetation (from mid of August until mid-November) and the second to wintry and prevernal vegetation (from mid-November until mid-March). Vernal and estival (from mid-March until mid-July) observations were not included as a decrease in bird activity on the site, perhaps as a consequence of more intense agricultural activities that altered the fields and disturbed the avifauna, and the changed behaviour during the breeding season of the common waxbills impeded the collection of data. The first field season lasted from the 21st of October to the 12th of November 2015 and the second from 19th of January to the 3rd of March 2016. To determine when to end each field season, there was a monitoring of the proportion of feeding events on each plant species on a cumulative plot (Figure 2). After the cumulative proportion of feeding on each plant species stabilized by reaching a plateau, observations were already sufficient to quantify the food preferences of the bird species accurately, thus, the field season could be ended. These two field seasons allowed me to sample vegetation from the serotinal/autumnal and wintry/prevernal seasons and, through our personal observations, it became clear that the plant species changed considerably across the three field seasons.

Each day, the observer walked, clock or anti-clockwise, around the circular observation path several times (Figure 1, blue line), detecting waxbills or serins visually and by means of their vocalizations. When waxbills or serins were located, and making use of binoculars, the observer checked whether there were any individuals feeding. Since these bird species usually feed as a group, and to avoid non-independent observations, only the plant from which one of the individuals was observed feeding (usually, the bird easiest to observe) on was identified, and then moved on along the observation path. I noted the time and exact location of each feeding observation on a map (Figure 1).

Observations were not noted when the act of feeding was not clearly visible or when birds were on the ground and it was not possible to determine whether the bird was feeding from fallen seeds or other materials. The identification of the plant species was made with the expert aid of a botanist (Paulo Alves), based on photographs or collected plants.

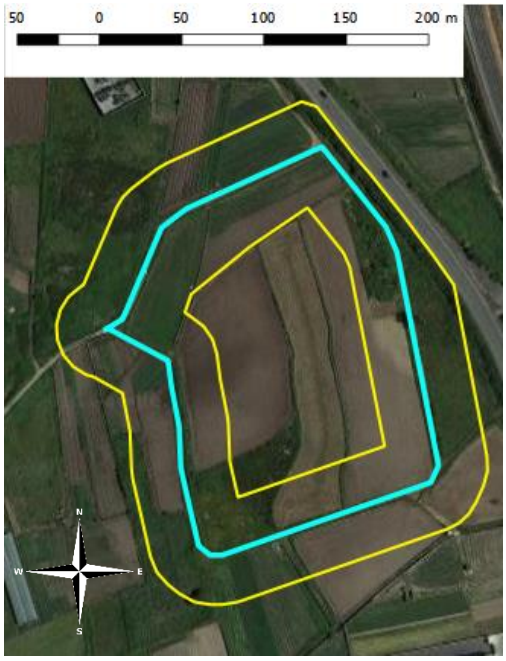

Figure 1: Observational field. In yellow, the 60 meter wide (30 meters to each side) observational area that circles around the field site for 710 meters in length. The blue line corresponds to the path walked by the observer.

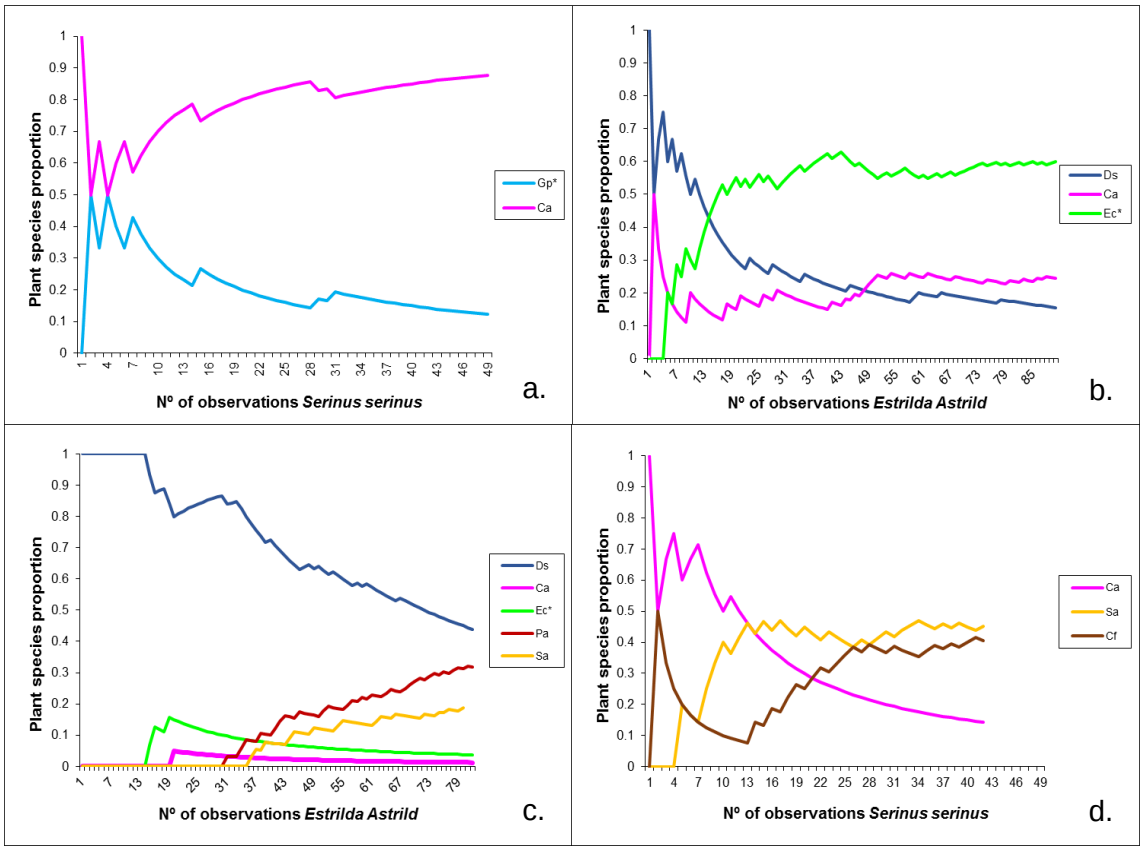

Figure 2: Cumulative plots of the proportion of feeding observations on each plant species by a. common waxbills and b. serins in the serotinal/autumnal field season, and c. common waxbills and d. serin in the wintry/prevernal field season. The symbol " * " marks the exotic species, according to the Atlas de las Plantas Alóctonas de España" (Sanz Elorza et

al. 2004). Plant species: Ds: *Digitaria sanguinalis*; Ca: *Chenopodium album*; Ec: *Echinochloa crus-galli*; Gp: *Galinsoga parviflora*; Pa: *Poa annua*; Sa: *Spergula arvensis*; Cf: *Chamaemelum fuscatum*.

2.2. Observational area: mapping and plant species

General Habitat Categories: Observations in parcels

For each field season, there was a characterization of the vegetation of the parcels within the observation sites (Table S2). To do so, the study site was first divided into parcels, where plant composition was relatively homogeneous, using the General Habitat Category (GHC) method (Bunce et al. 2011). Then, for each parcel, an inventory of the relative abundance of each plant species was made (Bunce et al. 2011, Table S2). These tasks were made with the expert aid of a botanist (Paulo Alves), approximately in the middle of each field season, in order to minimize the time distance between plant inventory and most feeding observations.

GHC parcels (Figure 3) were identified by systematically scanning the study area and subdividing it in parcels that share a set of dominant plant species. We used a simplified GHC method to define the contents of the parcels and to identify the most predominant plant species. The simplification of the methodology was the exclusive mapping of areal features, excluding linear and point features. To do this, each of the agricultural parcels was explored and attributed a GHC (e.g.: MPH = Medium Phanerophytes Evergreen) according to the dominant species life form or non/life form present or the agricultural practice in place. The next step was to identify the most common plant species in that parcel and determine a percentage of the occupancy of each of those (Bunce et al. 2011). These GHC parcels often coincided with the different agricultural parcels, but some uncultivated areas or agricultural parcels had to be divided into more than one GHC parcel. The area of each of the parcels was determined by mapping them with the Quantum Geographic Information System software (QGIS; Figure 3). The areas found were then intersected with the ca. 60-meter-wide observation corridor to obtain the observable area of each GHC parcel (Figure 4).

Figure 3: Representation of the GHC parcels (blue poligons).

Inventories: Season's plant species

Inventories of the relative abundance of plant species were made separately for each GHC parcel, and on each field season. The method for these inventories consists of scanning a GHC parcel visually and choosing a 2x2 m square that is representative of its vegetation's heterogeneity. Afterwards, it was necessary to identify all the plant species that were present in that square and count the number of individuals of each plant species observed in the 2x2 m square. Based on these counts, which were made separately for each of the individual GHC parcels, the relative abundance of each plant species across the entire study area was calculated as a weighted average of counts on all parcels. The average was weighted by the observable area of each parcel in order to take into account the parcels' different sizes. Thus, this metric "relative abundance" became a quantifier of the overall relative availability of each plant species across the entire observation area. When there were feeding observations on a plant species that was rare enough for it not to appear on the abundance inventories, the missing value was replaced with the lowest relative abundance value from that season. For the subset of plant species present in the study area and on which I observed at least one feeding event by waxbills or serins, the "Atlas de las Plantas Alóctonas de España" (Sanz Elorza et al. 2004) was consulted to ascertain whether those species were native or exotic to the Iberian Peninsula.

2.3. Analyses

Food preferences vs random feeding

To check if the studied bird species showed food preferences for certain plant species or, on the contrary, fed on edible plants proportionally to those plants' abundance in the study area, I compared the feeding observations with the relative abundance of those plants. Separately for common waxbills and serins, and separately for each field season, Goodness of Fit Chi-square tests were used to compare the observed counts of feeding events on each plant species with the relative abundance of those plant species in the study area. Plant species with zero feeding events might not have been edible in a season for a particular bird species and were, therefore, not included in these tests. The relative abundances of plants are used here as the expected values for the null hypothesis that birds feed on edible plants randomly, in proportion to their abundance in the study area.

Comparing food preferences between common waxbills and serins

For each field season, food preferences of common waxbills and serins were tested for similarity. With the use of Contingency Table Chi-Square tests, comparisons between the observed counts of feeding events on each plant species by waxbills and serins were made. Only plant species that had been fed upon at least once, by at least one bird species, during an observed season were used in these tests. Two characteristics of the eaten plant species were investigated (Table 2) in order to understand if there was any indication of a relationship between those traits and food preferences. These characteristics (Amerine & Kunkee 1968; http://www.cabi.org/isc/), culm and seed length, could be related to the body mass and the bill size, respectively, of the two bird species I observed feeding on them. Culm length represents the robustness of the plant, with a higher culm length related to a greater bird weight, and seed size represents the adaptation of the beak to the feeding on different seeds.

Comparing feeding overlap between common waxbills and serins in observed seasons

The feeding overlap between the two bird species was calculated for each season by first computing the product of the proportion of times that waxbills and serins were observed feeding on a given plant species, and then adding these products across all plant species. Overlap can vary between zero, which means that waxbills and serins always feed on different plant species, and one, which means that waxbills and serins

feed on the same plant species and in the same proportions. Feeding overlap between waxbills and serins was compared between the two field seasons using bootstrap estimates of confidence intervals for the differences in overlap between seasons. In order to perform this test, bootstraps (i.e., randomly sampled with replacement) from the feeding observations were made, separately for each species of bird and season, along with the calculation of the feeding overlap between waxbills and serins from these bootstrapped observations, separately for each field season, and, finally, the calculation of the difference between these feeding overlaps in the two field seasons. This bootstrap procedure was repeated 1000 times. To test if feeding overlaps were significantly larger than zero, it was assessed, separately for each field season, whether the unicaudal 95% confidence interval of bootstrapped feeding overlaps included zeroes. The proportion of these zeroes across the 1000 bootstrapped values of feeding overlap gives us the probability of the null hypothesis. In order to test for a significant difference in feeding overlap between the serotinal/autumnal and wintry/prevernal field seasons, it was determined whether the bicaudal 95% confidence interval of the bootstrapped differences in feeding overlap between seasons included zero. The probability of the null hypothesis (difference in overlap between seasons is 0) is given by 2 x the percentile for the value of zero across the 1000 bootstrapped differences in feeding overlap or, if the percentile is larger than 50%, by 2 x (1-percentile).

The role of exotic plants in the feeding overlap between waxbills and serins

Lastly, it was determined whether exotic plants significantly influenced feeding overlap between waxbills and serins. Separately, for each field season, a comparison of the feeding overlap between waxbills and serins was made, with their feeding overlap recalculated after removing observations of feeding on exotic plants. To do this, bootstrap estimates of the confidence interval for the difference in feeding overlap were used considering all plant species vs excluding exotic plant species. The probability of the null hypothesis (difference in overlap considering or not exotic plants is 0) is given by 2 x the percentile for the value zero across the 1000 bootstrapped differences in feeding overlap or, if the percentile is larger than 50%, by 2 x (1-percentile).

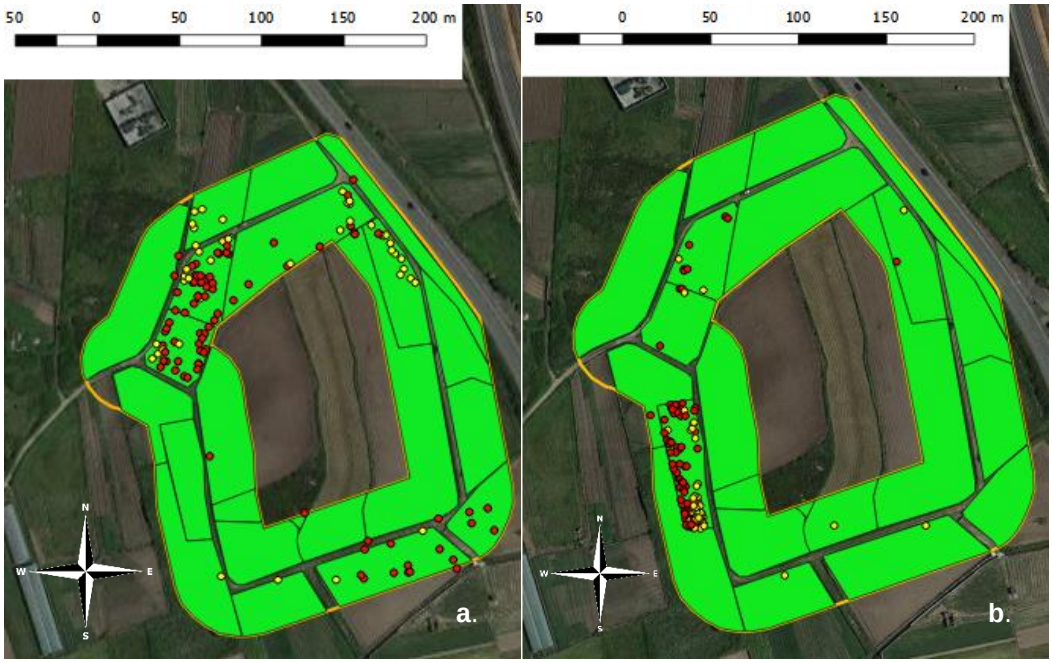

Figure 4: Representation of the observational areas and the circular path taken to gather the data. a. Serotinal/autumnal of feeding observations of waxbills (red dots) and serins (yellow dots); b. Wintry/prevernal observations (waxbill (red dots); serin (yellow dots)).

3. Results

90 observations of feeding events by common waxbills and 49 by serins were made during the first field season. Out of 90 different plant species identified in the field site (Table S2), it was observed that common waxbills and serins fed from only four species: *Chaenopodium album* (both bird species fed on this plant); *Echinochloa crus-galli* and *Digitaria sanguinalis* (common waxbill); *Galinsoga parviflora* (serin) (Table S1). 85 observations of feeding by waxbills and 42 by serins during the second field season were made. Out of 82 species of plants identified (Table S2), observations of common waxbills feeding on *Chenopodium album, Digitaria sanguinalis*, *Echinochloa crus-galli*, *Poa annua* and *Spergula arvensis*, and serins feeding on *Chamaemelum fuscatum*, *Chenopodium album* and *Spergula arvensis* (Table S1) were made. The observations were spatially identified as well and there were areas where the abundance of observations was greater than in others, especially during the wintry/prevernal season (Figure 4).

Food preferences vs random feeding

For the serotinal/autumnal season, the counts of feeding observation on the different plant species differed from the relative abundance of those same plant species, in

common waxbills (χ^2 = 48.343, P < 0.001, N = 90 feeding observations on the three plant species; Table 1), but not for serins (χ^2 = 1.727, P = 0.189, N = 49 feeding observations on two plant species; Table 1).

For the wintry/prevernal season, the counts of feeding observation on the different plant species differed from the relative abundance of those same plant species, in both common waxbills (χ^2 = 2586.128, P < 0.001, N = 85 feeding observations on five plant species) and serins (χ^2 = 73.364, P < 0.001, N = 42 feeding observations on three plant species; Table 1).

Comparing food preferences between common waxbills and serins

The Contingency Tables in the serotinal/autumnal field season showed significant differences amongst the preferences of both species (χ^2= 75.23 P < 0.001), with similar results in the wintry/prevernal field season (χ^2= 83.88 P < 0.001), which allowed us to say that the null hypothesis was rejected. The results obtained in Table 2 regarding the relationship between eaten plant species' traits and food preferences from both bird species were inconclusive, as both bird species foraged on plants with different culm lengths and seed sizes.

Comparing feeding overlap between common waxbills and serins in observed seasons

The feeding overlap between waxbills and serins on the serotinal/autumnal season was 21.45%, because both species fed on *Chenopodium album* (Figure 5). Feeding overlap in the wintry/prevernal field season decreased, with a value of 8.68%, with common feeding on *Chenopodium album* and *Spergula arvensis*, which contributed to a 0.17% and a 8.51% overlap, respectively (Figure 5). The bootstrap confidence interval for this difference in feeding overlap did not include zeros (P < 0.001), giving the significant decrease in feeding overlap, in the wintry/prevernal season, statistical support. Furthermore, the bootstrap confidence interval for the feeding overlap observed in the serotinal/autumnal season was significantly different from zero (P < 0.001), however, it was not significantly different from zero in the wintry/prevernal season (P = 0.226).

The role of exotic plants in the feeding overlap between waxbills and serins

Serins were observed feeding on the exotic plant species *Galinsoga parviflora*, and waxbills on *Echinochloa crus-galli*, during the serotinal/autumnal field season. The

feeding overlap between waxbills and serins on that season was 21.45%, but, if recalculated excluding observations from these plants, it would be about three times higher, at 61.11%. The bootstrap confidence interval for the difference in feeding overlap including vs. excluding observations on feeding on these plants did not include zeros ($P < 0.001$), giving statistical evidence to the significant alleviation that feeding on exotic plants has on feeding overlap between these bird species during the serotinal/autumnal season. *Echinochloa crus-galli* was observed being foraged on by waxbills during the wintry/prevernal season. The feeding overlap between waxbills and serins on that season was 8.68%, but, if recalculated excluding observations from this exotic plant, it would increase, very slightly, to 9.00%. The bootstrap confidence interval for the difference in feeding overlap including vs. excluding observations of feeding events on these plants included zeros ($P = 0.958$), giving no statistical evidence to the significant alleviation that feeding on exotic plants has on feeding overlap between these bird species during the wintry/prevernal season.

4. Discussion

It was found that waxbills and serins did not feed on edible plant species according to their relative abundance, showing food preferences instead. Only in the serotinal/autumnal season did serins feed on edible plants approximately proportionally to their relative abundance, which could have been coincidental, given that only two plant species were observed on their diet during this season. The food preferences of waxbills and serins were statistically different and the overlap in feeding between the two bird species was low and decreased significantly from the serotinal/autumnal season (21.45% overlap) to the wintry/prevernal one (8.68% overlap). Since the winter time is, most likely, where food could be more limiting, the already low and, later on, decreasing overlap in feeding between serins and waxbills suggests little potential for ecologically relevant competition for food among these bird species. The lack of competition agrees with results discovered in, e.g., exotic black-headed weavers (*Ploceus melanocephalus*) and two ecologically similar native species, which were found to have overlap in resource requirements, but did not compete for them (Sullivan et al., 2014). The role of exotic plant species in the alleviation of the feeding overlap between serins and waxbills was very high during the first season due to the fact that both bird species fed on exotic plant species, but was less important in the wintry/prevernal season, where feeding on the exotic plant species was a rare event.

Table 1: Values used for the Goodness of fit calculations: Observed and expected values for all the field seasons and the Chi-Square results per bird species in each season.

Serotinal/Autumnal		
Plant species	Observed feeding events	Predicted feeding events
Common waxbill, Serotinal/Autumnal season ($\chi2$ = 48.343, P < 0.001, N = 90 feeding observations)		
Chenopodium album	24	8.9
Echinochloa crus-galli	52	41.0
Digitaria sanguinalis	14	42.1
Serin, Serotinal/Autumnal season ($\chi2$ = 1.727, P = 0.189, N = 49 feeding observations)		
Chenopodium album	43	39.3
Galinsoga parviflora	6	9.7
Wintry/Prevernal		
Common waxbill, Wintry/Prevernal season ($\chi2$ = 2586.128, P < 0.001 , N = 85 feeding observations)		
Chenopodium album	1	0.5
Echinochloa crus-galli	3	0.5
Digitaria sanguinalis	36	0.5
Poa annua	29	71.6
Spergula arvensis	16	13.0
Serin, Wintry/Prevernal season ($\chi2$ = 73.364, P < 0.001, N = 42 feeding observations)		
Chenopodium album	6	0.5
Spergula arvensis	19	12.4
Chamaemelum fuscatum	17	29.2

Even though exotic plant species appear to not have provided any aid in alleviating the food overlap during the wintry/prevernal season, the diversification in food choices by both species shows a different approach to dealing with more stressful periods. It is known some bird species, namely migratory, have high diet flexibility because of the harsh conditions they face yearly (Marshall et al., 2016).

Waxbills and serins relied on both native and exotic plant species for food. Their diet consisted of seeds from grasses and plants found in the study area (Table 1). I tried to understand if any of the eaten plant species' physical characteristics were influencing the different food preferences from each bird species, such as culm length and seed

size (Table 2). However, I could not find, among the analysed characteristics, any indication that they were influencing food preferences. This indicates that these weight and bill size-related traits do not have any relationship to the food preferences observed. My observations on feeding options in waxbills and serins agree with the suggestion presented by Batalha et al. (2013) regarding the occupation of an ecologically differentiated niche by common waxbills relative to the native species in Iberia. Despite the fact that the European serin is the most similar native bird species to common waxbills in diet and foraging habits, the two species fed, mostly, on different plant species.

Table 2: Characteristics of the observed eaten plant species that might influence food preferences of the two bird species (the " * " mark represents the exotic plant species). Coloured highlights: red – foraged on by common waxbills; yellow – foraged on by serins; orange – foraged on by both species.

Species	Morphological relevant aspects (centimeters)	
	Culm length	Caryopsis/achene size
Chamaemelum fuscatum	6.0-40.0	0.01-0.14
Chenopodium album	20.0-200.0	0.15
Digitaria sanguinalis	20.0-60.0	0.10-0.16
*Echinocloa crus-galli**	20.0-200.0	0.13-0.22
*Galinsoga parviflora**	20.0-80.0	0.11-0.20
Poa annua	10.0-40.0	0.4
Spergula arvensis	15.0-60.0	0.15

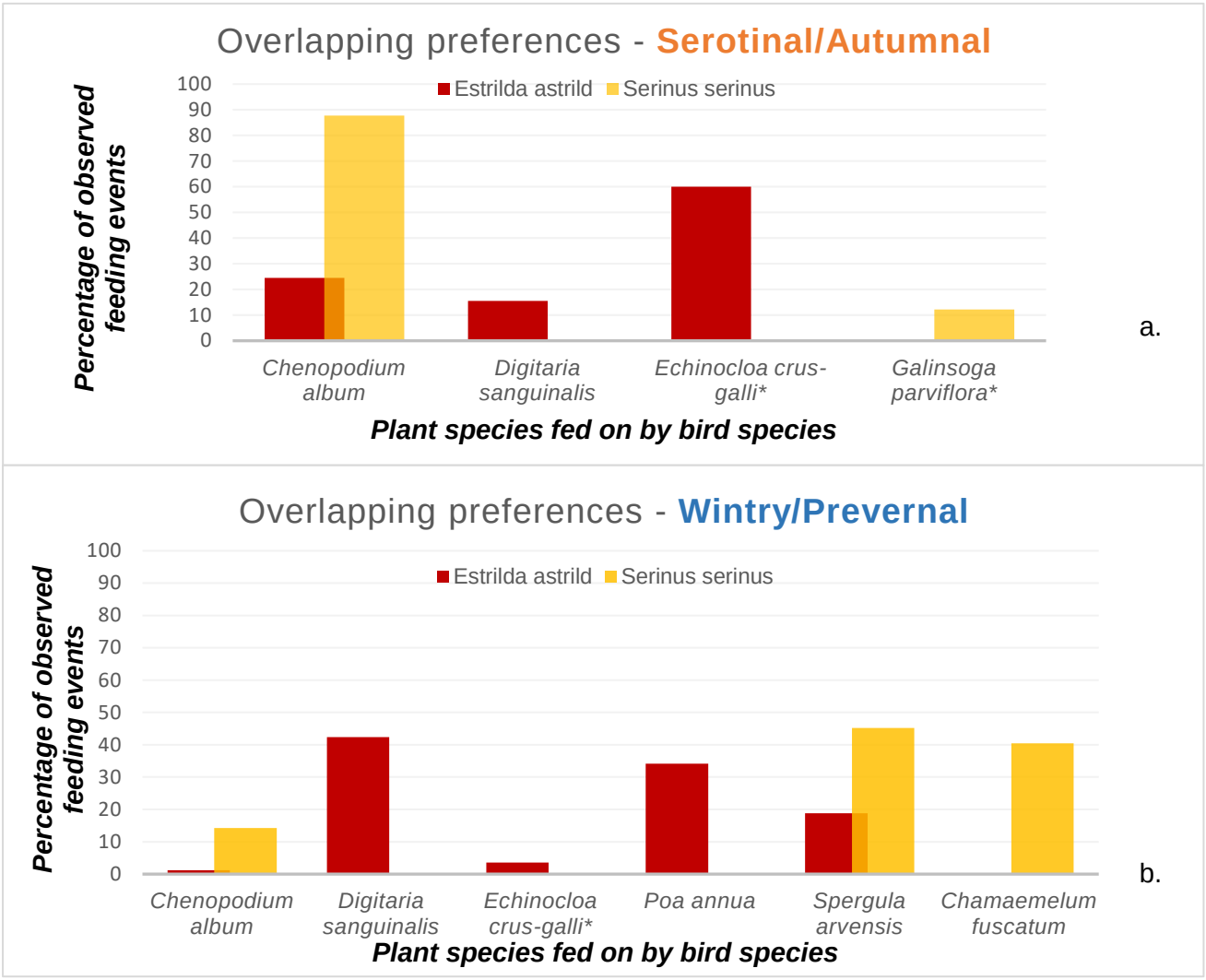

Figure 5: Proportion of feeding overlap between both bird species and the plant species (plants marked with " * " are exotic species) they fed on during the: a. Serotinal/Autumnal season; b. Wintry/Prevernal season.

If the feeding preferences' overlap between the two bird species is small, then this same feeding overlap must be even more dissimilar when up against the remaining native passerines, making the hypothesis that common waxbills occupy a highly differentiated niche a conceivable conclusion. The assumption that these two species occupy different niches also shows there is an indication for low competition potential, which is to be expected based on previous research that indicates that disturbed environments not only create new resources easily exploited by exotic species, e.g., exotic bird species are correlated with areas disturbed by humans which create opportunistic resources (Sullivan et al., 2015) and also decrease the competitive pressure (Shea & Chesson 2002; Tilman, 2004).

Another result that suggests that the two species have low potential for ecologically detrimental competition for food is that the already low feeding overlap between waxbills and serins during the serotinal/autumnal season decreased in the

wintry/prevernal season. In terms of foraging and energetic balance, the winter should be the hardest and most stressful period of the year because of the limited food resources and the more severe weather (Stapanian et al., 1999; Castro & Fernández-Nuñez, 2016). Hence, while feeding on the same plants during a time of abundance may not be critical, the two species feeding on the same plants during the winter time could contribute to a competitive depletion of a resource with negative consequences for either waxbills or serins (Sol, 2016). The wintry/prevernal season was, however, the season that revealed the lowest percentage of feeding overlap between the two bird species. The low overlap in this season might be related to the changes in diet that occurred to compensate for the lack of both bird species' preferred food resources, something that is known to happen in migratory birds, as their diet corresponds to the availability of resources and to their immediate energetic needs (Marshall et al., 2016). This means that, even when food is hypothesized to be scarcer and when these bird species could converge on the same remaining edible plants, waxbills and serins continued to choose different plant species to rummage on and, in doing so, reduced the feeding overlap to approximately zero. In addition to this, there were no obvious alarm calls or attacks from one species towards the other and they mostly shared the same feeding areas without any proximity issues (pers. obs.). During the winter, despite the low feeding overlap, the fact is that both species mostly shared the same parcel throughout the observation period (pers. obs.; Figure 4). Even though there was some obvious separation during feeding events on both seasons (Figure 4), both species could share the same areas while never being part of the same group (pers. obs.). Hence, common waxbills and serins appear not to have a problem with proximity, which has been proven to be effective, when in flocks, in reducing predation risk and increasing the efficiency of foraging (Munoz, 2016). This suggests very little potential for detrimental competition for food between waxbills and serins, which is congruent with the fact that species with the same phenotype and low resource overlap will compete less (Sol, 2016).

This exotic species, rather than compete with a native species, as is usually assumed in invasion ecology (Bruno et al., 2013; Batalha et al., 2013; Baker et al., 2014; Martin-Albarracin et al., 2015), seems to occupy a vacant and ecologically differentiated niche, based on comparisons in food preferences and feeding overlaps with the native serin. This is backed up by research, as data regarding exotic and native bird species' interactions indicates a lack of evidence of competition between them and also because a very likely explanation for the exotic bird species being able to arrive at most

new destinations without competing is because of either vacant niches or underexploited resources (Tilman, 2004; Sol et al., 2012), as was mentioned before.

Positive interactions between exotic and other exotic species were also considered, in order to be able to cast some insight into whether there is facilitation, by exotic plant species, in the maintenance of the common waxbill in the invaded range. Common waxbills and serins fed on exotic plant species during the serotinal/autumnal season, which significantly reduced the feeding overlap between them. Common waxbills, in particular, fed mostly on exotic plant species (60% of observed feeding events in the serotinal/autumnal season), while serins depended less on exotic plant species (12.25% of observed feeding events in the serotinal/autumnal season). This shows an intriguing association between the exotic bird species, the common waxbill, and the exotic plant species present in this agricultural landscape. Whether this connection is enough to reveal a facilitation effect of exotic plant species on the biological invasion by waxbills is up for discussion. Based on these results, I can hypothesize that exotic plant species facilitate the invasion of common waxbills by providing them with food resources that are not fully explored by native species with similar feeding habits, size and weight. As observations were made on an agricultural field that was highly modified by humans, this facilitation by exotic plant species fits into the context of the exploration of new/alternative food resources introduced by men's disturbance (Sol et al., 2012). The disruption created by agricultural fields creates a disequilibrium in the previous ecosystem and leads to the blooming of new resources (Shea & Chesson 2002; Tilman, 2004). New resources in an ecosystem in disequilibrium conditions often go unexploited by the previously present native species, as they already have their preferred feeding habits (Sol, 2016). Therefore, exotic species may find a niche which is available and provides the food resources they need to enter the system (Sanz-Aguillar et al., 2015). Common waxbills' reliance on exotic plant species shows that the disturbance created by men in the native territory, which increases available niches for new species to explore, might have given them the chance to do so. Since serins did not massively depend on this resource, then exotic species are able to explore it and take advantage of a niche that was vacant, thus avoiding potential competition for resources.

5. Conclusion

As is deemed necessary in the study of biological invasions by Sol et al. (2012), our study focused on interactions between exotic-exotic and exotic-native coexisting species. Research on invasion ecology consistently prioritizes competitive interactions (Schoener, 1982; Martin-Albarracin et al., 2015), considering them to be the main structural basis of communities (Bruno et al., 2003; Bulleri et al., 2008; Batalha et al., 2013) as well as what shapes most relationships within communities (Baker et al., 2014). Despite the potential importance of competition, it is undeniable that birds can affect other bird species in incredibly varied ways, and one of them is the changes in availability of food resources, seeing as food can be one of the most limiting factors for most species (Shochat et al., 2006; Chupp & Battaglia 2016). Competition is, nonetheless, an incomplete expression of community interactions (Bruno et al., 2003), as its importance is representative of a small part of ecosystem relationships, but not their entirety. Facilitative interactions have gained a growing sum of adepts in the study of the biology of invasions (Bertness & Callaway 1994). It is considered more complete to include these interactions in studies (Tassin & Kull 2014) than to focus, solely, on negative consequences and ignore other types of relationships that can impact the communities just as much.

Current literature discusses the three topics discussed in this thesis: competition is not the main pillar of ecosystems, rather, an array of interactions are responsible for the structure of ecosystems; vacant niches or underexploited resources allow exotic species to occupy places in communities; facilitative interactions between exotic species can alleviate potential competitive behaviour by providing alternative food resources that go unexplored by native species. This thesis confirms these and goes beyond by giving a better understanding, in the studied area, of the effects of the common waxbill as an exotic species and by introducing the role exotic plant species have in invasibility facilitation through the creation of food resources. The lack of evidence for potential interspecific competition through the occupation of a vacant ecologically differentiated niche, when compared to that of serins, and the potential facilitative role of exotic plant species present in the study area indicate that this exotic bird species might have a neutral or positive impact in the ecosystem where it arrived.

In order to deepen what was studied here and gain access to more information on common waxbills, it would be profitable to:

- Do a follow up study to verify that the food preferences remain the same in other areas with different available resources, thus further confirming their preferences for specific plant species;

- Search for more characteristics of the plant species that were eaten and discover which traits may indicate preferences towards some (e.g., nutritional values related to energetic needs);

- Test how the variation in the season's climate might affect food choices by investigating the nutritional value of the plants that were eaten and comparing those choices in different seasons (including the most stressful seasons: the winter and the breeding season);

- Test how human disturbance, by land use and the application of different land organization throughout the year, affects the food preferences and the distribution of feeding events of the studied bird species.

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Annexes

Table S1: Observations during both seasons. The purple line marks the time in between both seasons. In each column: the bird species that was observed feeding (Ea: *Estrilda astrild*; Ss: *Serinus Serinus*), the day-month-year of each observation; the hour-minute of each observation (summer and winter Greenwich Mean Time); the plant species where feeding occurred (Ds: *Digitaria sanguinalis*; Ca: *Chenopodium album*; Ec: *Echinochloa crus-galli*; Gp: *Galinsoga parviflora*; Pa: *Poa annua*; Sa: *Spergula arvensis*; Cf: *Chamaemelum fuscatum*); the area where the observation occurred based on the GHC parceling.

Bird species	Date	Time (GMT+1)	Time (GMT+0)	Plant Species	Season/Area
Ea	21-10-15	8:07:00 AM		Ds	AA2
Ea	21-10-15	8:28:00 AM		Ca	AA2
Ea	21-10-15	8:55:00 AM		Ds	AA1
Ea	21-10-15	9:02:00 AM		Ds	AA1
Ea	21-10-15	9:03:00 AM		Ec	AA2
Ea	21-10-15	9:11:00 AM		Ds	AA2
Ea	21-10-15	9:20:00 AM		Ec	AA12
Ea	21-10-15	9:37:00 AM		Ds	AA1
Ea	21-10-15	10:12:00 AM		Ec	AA2
Ea	21-10-15	11:00:00 AM		Ca	AA1
Ea	21-10-15	11:02:00 AM		Ds	AA5
Ea	21-10-15	11:04:00 AM		Ec	AA2
Ss	21-10-15	9:30:00 AM		Ca	AA1
Ss	21-10-15	9:33:00 AM		Gp	AA3
Ss	21-10-15	9:44:00 AM		Ca	AA2
Ss	21-10-15	10:01:00 AM		Gp	AA3
Ss	21-10-15	10:10:00 AM		Ca	AA1
Ss	21-10-15	10:30:00 AM		Ca	AA5
Ss	21-10-15	10:35:00 AM		Gp	AA3
Ea	22-10-15	8:04:00 AM		Ec	AA1
Ea	22-10-15	8:25:00 AM		Ec	AA19
Ea	22-10-15	8:32:00 AM		Ec	AA2
Ea	22-10-15	8:38:00 AM		Ec	AA21
Ea	22-10-15	8:40:00 AM		Ec	AA21
Ea	22-10-15	8:42:00 AM		Ca	AA1
Ea	22-10-15	8:45:00 AM		Ec	AA1
Ea	22-10-15	8:50:00 AM		Ec	AA5
Ea	22-10-15	8:54:00 AM		Ca	AA5
Ea	22-10-15	9:15:00 AM		Ec	AA1
Ea	22-10-15	9:54:00 AM		Ds	AA5
Ea	22-10-15	10:25:00 AM		Ec	AA1
Ss	22-10-15	8:11:00 AM		Ca	AA5
Ss	22-10-15	8:34:00 AM		Ca	AA2
Ss	22-10-15	8:36:00 AM		Ca	AA1
Ss	22-10-15	8:50:00 AM		Ca	AA5

Ss	22-10-15	8:57:00 AM		Ca	AA8
Ss	22-10-15	9:07:00 AM		Ca	AA17
Ss	22-10-15	9:19:00 AM		Ca	AA1
Ss	22-10-15	9:25:00 AM		Gp	AA5
Ss	22-10-15	9:29:00 AM		Ca	AA5
Ss	22-10-15	9:50:00 AM		Ca	AA1
Ea	23-10-15	8:00:00 AM		Ec	AA2
Ea	23-10-15	8:19:00 AM		Ca	AA5
Ea	23-10-15	8:30:00 AM		Ec	AA2
Ea	23-10-15	8:33:00 AM		Ds	AA2
Ea	23-10-15	8:59:00 AM		Ca	AA1
Ea	23-10-15	9:10:00 AM		Ec	AA2
Ea	23-10-15	9:45:00 AM		Ec	AA1
Ea	23-10-15	10:07:00 AM		Ec	AA1
Ea	23-10-15	10:40:00 AM		Ec	AA1
Ss	23-10-15	8:15:00 AM		Ca	AA7
Ss	23-10-15	8:23:00 AM		Ca	AA2
Ss	23-10-15	8:50:00 AM		Ca	AA7
Ss	23-10-15	8:56:00 AM		Ca	AA2
Ss	23-10-15	9:25:00 AM		Ca	AA7
Ss	23-10-15	9:55:00 AM		Ca	AA7
Ss	23-10-15	10:35:00 AM		Ca	AA7
Ss	23-10-15	10:48:00 AM		Ca	AA12
Ea	27-10-15		8:21:00 AM	Ec	AA1
Ea	27-10-15		8:30:00 AM	Ds	AA1
Ea	27-10-15		8:43:00 AM	Ec	AA12
Ea	27-10-15		8:54:00 AM	Ec	AA1
Ea	27-10-15		9:37:00 AM	Ec	AA12
Ea	27-10-15		10:07:00 AM	Ec	AA1
Ss	27-10-15		9:09:00 AM	Ca	AA12
Ss	27-10-15		9:25:00 AM	Ca	AA7
Ss	27-10-15		9:51:00 AM	Ca	AA2
Ea	30-10-15		7:23:00 AM	Ec	AA2
Ea	30-10-15		7:45:00 AM	Ca	AA1
Ea	30-10-15		7:50:00 AM	Ec	AA2
Ea	30-10-15		8:17:00 AM	Ec	AA2
Ea	30-10-15		8:34:00 AM	Ca	AA5
Ea	30-10-15		8:45:00 AM	Ds	AA2
Ea	30-10-15		8:47:00 AM	Ca	AA2
Ea	30-10-15		8:48:00 AM	Ec	AA2
Ea	30-10-15		8:57:00 AM	Ca	AA12
Ea	30-10-15		9:05:00 AM	Ca	AA7
Ea	30-10-15		9:25:00 AM	Ca	AA12
Ss	30-10-15		8:12:00 AM	Gp	AA3
Ss	30-10-15		8:14:00 AM	Ca	AA4

Ss	30-10-15	9:10:00 AM	Gp	AA1
Ss	30-10-15	9:12:00 AM	Ca	AA12
Ea	02-11-15	7:30:00 AM	Ca	AA2
Ea	02-11-15	7:31:00 AM	Ec	AA2
Ea	02-11-15	7:32:00 AM	Ec	AA1
Ea	02-11-15	7:33:00 AM	Ca	AA1
Ea	02-11-15	7:34:00 AM	Ec	AA1
Ea	02-11-15	7:52:00 AM	Ec	AA12
Ea	02-11-15	8:04:00 AM	Ec	AA2
Ea	02-11-15	8:08:00 AM	Ca	AA1
Ea	02-11-15	8:10:00 AM	Ds	AA5
Ea	02-11-15	8:35:00 AM	Ds	AA1
Ea	02-11-15	8:38:00 AM	Ec	AA1
Ea	02-11-15	8:45:00 AM	Ca	AA7
Ea	02-11-15	9:00:00 AM	Ec	AA2
Ea	02-11-15	9:40:00 AM	Ec	AA1
Ss	02-11-15	7:38:00 AM	Ca	AA5
Ss	02-11-15	7:41:00 AM	Ca	AA7
Ss	02-11-15	8:14:00 AM	Ca	AA5
Ss	02-11-15	8:17:00 AM	Ca	AA7
Ss	02-11-15	8:43:00 AM	Ca	AA5
Ss	02-11-15	8:57:00 AM	Ca	AA16
Ss	02-11-15	9:04:00 AM	Ca	AA2
Ea	03-11-15	7:50:00 AM	Ds	AA1
Ea	03-11-15	7:51:00 AM	Ec	AA1
Ea	03-11-15	8:15:00 AM	Ec	AA1
Ea	03-11-15	8:25:00 AM	Ca	AA11
Ea	03-11-15	8:33:00 AM	Ec	AA1
Ss	03-11-15	7:43:00 AM	Ca	AA5
Ea	10-11-15	7:43:00 AM	Ec	AA5
Ea	10-11-15	7:44:00 AM	Ec	AA6
Ea	10-11-15	7:45:00 AM	Ec	AA7
Ea	10-11-15	7:55:00 AM	Ec	AA11
Ea	10-11-15	8:02:00 AM	Ec	AA12
Ea	10-11-15	8:10:00 AM	Ca	AA2
Ea	10-11-15	8:11:00 AM	Ec	AA2
Ea	10-11-15	8:34:00 AM	Ec	AA12
Ea	10-11-15	8:35:00 AM	Ds	AA12
Ea	10-11-15	9:04:00 AM	Ec	AA11
Ea	10-11-15	9:05:00 AM	Ca	AA12
Ea	10-11-15	9:40:00 AM	Ec	AA11
Ea	10-11-15	9:45:00 AM	Ec	AA2
Ea	10-11-15	9:48:00 AM	Ca	AA1
Ea	10-11-15	9:50:00 AM	Ec	AA2
Ss	10-11-15	7:30:00 AM	Ca	AA2

Ss	10-11-15		8:14:00 AM	Ca	AA1
Ss	10-11-15		8:57:00 AM	Ca	AA7
Ss	10-11-15		9:09:00 AM	Ca	AA1
Ss	10-11-15		9:47:00 AM	Ca	AA1
Ea	12-11-15		7:35:00 AM	Ec	AA11
Ea	12-11-15		7:50:00 AM	Ca	AA1
Ea	12-11-15		8:01:00 AM	Ec	AA12
Ea	12-11-15		8:20:00 AM	Ca	AA14
Ea	12-11-15		8:23:00 AM	Ec	AA12
Ea	12-11-15		8:50:00 AM	Ec	AA12
Ss	12-11-15		7:42:00 AM	Ca	AA7
Ss	12-11-15		7:44:00 AM	Ca	AA5
Ss	12-11-15		8:12:00 AM	Ca	AA2
Ss	12-11-15		8:36:00 AM	Ca	AA1

Bird Species	Date	Time (GMT+1)	Time (GMT+0)	Plant Species	Season/Area
Ea	19-01-16		8:12:00 AM	Ds	WA18
Ea	19-01-16		8:35:00 AM	Ds	WA18
Ea	19-01-16		9:07:00 AM	Ds	WA18
Ea	20-01-16		8:55:00 AM	Ds	WA18
Ea	23-01-16		8:17:00 AM	Ds	WA18
Ea	23-01-16		8:30:00 AM	Ds	WA18
Ea	23-01-16		8:45:00 AM	Ds	WA18
Ea	23-01-16		9:00:00 AM	Ds	WA18
Ss	23-01-16		8:48:00 AM	Ca	WA12
Ea	26-01-16		8:00:00 AM	Ds	WA18
Ea	26-01-16		8:34:00 AM	Ds	WA18
Ea	26-01-16		8:50:00 AM	Ds	WA18
Ea	26-01-16		9:01:00 AM	Ds	WA18
Ea	26-01-16		9:15:00 AM	Ds	WA18
Ea	26-01-16		9:15:00 AM	Ds	WA18
Ea	26-01-16		9:40:00 AM	Ec	WA2
Ea	26-01-16		9:57:00 AM	Ec	WA2
Ss	26-01-16		9:40:00 AM	Cf	WA18
Ss	26-01-16		9:59:00 AM	Ca	WA1
Ea	27-01-16		8:25:00 AM	Ds	WA18
Ea	27-01-16		8:45:00 AM	Ds	WA18
Ea	27-01-16		9:00:00 AM	Ec	WA7
Ea	29-01-16		8:20:00 AM	Ca	WA1
Ea	29-01-16		8:26:00 AM	Ds	WA18
Ea	29-01-16		8:58:00 AM	Ds	WA18
Ea	29-01-16		9:02:00 AM	Ds	WA1
Ea	29-01-16		9:30:00 AM	Ds	WA18
Ea	29-01-16		9:35:00 AM	Ds	WA18
Ss	29-01-16		10:15:00 AM	Ca	WA1

Ea	01-02-16	8:00:00 AM	Ds	WA18
Ea	01-02-16	8:25:00 AM	Ds	WA18
Ea	01-02-16	8:40:00 AM	Ds	WA1
Ea	02-02-16	7:50:00 AM	Ds	WA18
Ea	02-02-16	8:15:00 AM	Ds	WA18
Ea	02-02-16	8:38:00 AM	Pa	WA18
Ea	02-02-16	8:50:00 AM	Ds	WA1
Ea	02-02-16	9:45:00 AM	Ds	WA18
Ss	02-02-16	9:45:00 AM	Sa	WA18
Ea	03-02-16	8:15:00 AM	Pa	WA18
Ea	05-02-16	8:42:00 AM	Sa	WA18
Ea	05-02-16	8:45:00 AM	Sa	WA18
Ea	05-02-16	8:47:00 AM	Pa	WA18
Ea	05-02-16	8:47:00 AM	Sa	WA18
Ea	05-02-16	8:47:00 AM	Ds	WA18
Ss	05-02-16	8:12:00 AM	Ca	WA2
Ss	05-02-16	8:25:00 AM	Ca	WA7
Ss	05-02-16	8:38:00 AM	Sa	WA18
Ss	05-02-16	8:47:00 AM	Sa	WA13
Ea	16-02-16	7:58:00 AM	Pa	WA18
Ea	16-02-16	8:10:00 AM	Pa	WA18
Ea	16-02-16	8:38:00 AM	Pa	WA18
Ea	16-02-16	8:39:00 AM	Sa	WA18
Ss	16-02-16	8:39:00 AM	Sa	WA18
Ss	16-02-16	9:27:00 AM	Ca	WA1
Ea	18-02-16	7:55:00 AM	Sa	WA18
Ea	18-02-16	8:10:00 AM	Pa	WA18
Ea	18-02-16	8:10:00 AM	Ds	WA18
Ea	18-02-16	8:30:00 AM	Ds	WA18
Ss	18-02-16	7:56:00 AM	Sa	WA18
Ss	18-02-16	8:15:00 AM	Sa	WA18
Ss	18-02-16	8:45:00 AM	Cf	WA18
Ss	18-02-16	8:45:00 AM	Sa	WA18
Ss	18-02-16	8:55:00 AM	Cf	WA18
Ss	18-02-16	8:55:00 AM	Sa	WA18
Ss	18-02-16	9:05:00 AM	Cf	WA18
Ss	18-02-16	9:20:00 AM	Cf	WA18
Ss	18-02-16	9:23:00 AM	Sa	WA18
Ss	18-02-16	10:20:00 AM	Cf	WA18
Ea	19-02-16	8:02:00 AM	Sa	WA18
Ea	19-02-16	8:02:00 AM	Ds	WA18
Ea	19-02-16	8:05:00 AM	Pa	WA18
Ea	19-02-16	8:20:00 AM	Pa	WA18
Ea	19-02-16	8:20:00 AM	Ds	WA18
Ea	19-02-16	8:22:00 AM	Sa	WA18

Ea	19-02-16	9:35:00 AM	Sa	WA18
Ea	19-02-16	9:37:00 AM	Pa	WA18
Ea	19-02-16	9:55:00 AM	Pa	WA18
Ea	19-02-16	9:58:00 AM	Ds	WA18
Ea	22-02-16	7:50:00 AM	Pa	WA18
Ea	22-02-16	8:20:00 AM	Ds	WA18
Ea	22-02-16	8:24:00 AM	Pa	WA18
Ea	22-02-16	8:26:00 AM	Sa	WA18
Ea	22-02-16	8:40:00 AM	Sa	WA18
Ea	22-02-16	8:43:00 AM	Pa	WA18
Ea	22-02-16	8:53:00 AM	Pa	WA18
Ea	22-02-16	8:55:00 AM	Sa	WA18
Ea	22-02-16	8:59:00 AM	Ds	WA18
Ss	22-02-16	8:40:00 AM	Cf	WA18
Ss	22-02-16	8:50:00 AM	Sa	WA18
Ss	22-02-16	8:53:00 AM	Cf	WA18
Ss	22-02-16	9:55:00 AM	Cf	WA18
Ea	23-02-16	7:58:00 AM	Pa	WA18
Ea	23-02-16	8:02:00 AM	Pa	WA18
Ea	23-02-16	8:20:00 AM	Pa	WA18
Ea	23-02-16	8:30:00 AM	Pa	WA18
Ea	23-02-16	8:36:00 AM	Sa	WA18
Ea	23-02-16	8:53:00 AM	Pa	WA18
Ss	23-02-16	7:51:00 AM	Cf	WA18
Ss	23-02-16	7:53:00 AM	Sa	WA18
Ss	23-02-16	8:50:00 AM	Cf	WA18
Ss	23-02-16	8:50:00 AM	Sa	WA18
Ss	23-02-16	8:53:00 AM	Sa	WA18
Ea	29-02-16	7:55:00 AM	Pa	WA18
Ea	29-02-16	8:00:00 AM	Sa	WA18
Ea	29-02-16	8:12:00 AM	Pa	WA18
Ea	29-02-16	8:25:00 AM	Sa	WA18
Ea	29-02-16	8:27:00 AM	Pa	WA18
Ea	29-02-16	8:42:00 AM	Pa	WA18
Ea	29-02-16	8:45:00 AM	Sa	WA18
Ea	29-02-16	8:55:00 AM	Pa	WA18
Ss	29-02-16	8:29:00 AM	Cf	WA18
Ss	29-02-16	8:31:00 AM	Sa	WA18
Ea	03-03-16	7:59:00 AM	Sa	WA18
Ea	03-03-16	8:13:00 AM	Pa	WA18
Ea	03-03-16	8:28:00 AM	Pa	WA18
Ea	03-03-16	8:43:00 AM	Pa	WA18
Ea	03-03-16	9:00:00 AM	Pa	WA18
Ss	03-03-16	8:02:00 AM	Sa	WA18
Ss	03-03-16	8:14:00 AM	Sa	WA18

Ss	03-03-16	8:16:00 AM	Cf	WA18
Ss	03-03-16	8:28:00 AM	Cf	WA18
Ss	03-03-16	8:29:00 AM	Sa	WA18
Ss	03-03-16	8:42:00 AM	Cf	WA18
Ss	03-03-16	8:42:00 AM	Sa	WA18
Ss	03-03-16	8:58:00 AM	Cf	WA18
Ss	03-03-16	9:32:00 AM	Cf	WA18
Ss	03-03-16	9:33:00 AM	Sa	WA18

Table S2: Plant species identified using the simplified inventory method along with the relative abundance of each species.

Serotinal/autumnal Plant Species	Relative abundance	Wintry/prevernal Plant Species	Relative abundance
Agrostis capillaris	5.259703149	*Agrostis capillaris*	4.656263132
Allium ampeloprasum var. porrum	1.464331517	*Allium ampeloprasum var. porrum*	1.830414396
Amaranthus powellii	1.664215409	*Allim cepa*	2.004034655
Andryala integrifolia	0.045349859	*Ammi majus*	0.044020306
Anredera cordifolia	0.188378702	*Anagallis arvensis*	0.080356424
Ballota nigra	0.03767574	*Andryala integrifolia*	0.044020306
Brassica oleracea	3.540488622	*Anredera cordifolia*	0.188378702
Brassica rapa	0.610794063	*Arctotheca calendula*	0.392166063
Bromus catharticus	0.034323145	*Ballota nigra*	0.03767574
Bryonia dioica	0.188378702	*Brassica oleracea*	2.071742501
Calendula arvensis	0.222964492	*Brassica rapa*	1.832382188
Calystegia sepium	0.440203061	*Bromus catharticus*	0.034323145
Calystegia silvatica	0.188378702	*Calendula arvensis*	0.034323145
Cardamine hirsuta	0.081685976	*Cardamine hirsuta*	0.077883211
Chamaemelum fuscatum	0.459271868	*Cerastium glomeratum*	0.063967679
Chenopodium album	5.635558037	*Chamaemelum fuscatum*	1.886576771
Chenopodium ambrosioides	0.044020306	*Chamaemelum mixtum*	0.034596132
Chrysanthemum segetum	0.24370252	*Chrysanthemum segetum*	0.782409786
Cirsium filipendulum	0.012684504	*Cirsium filipendulum*	0.049020622
Cirsium vulgare	0.044020306	*Cirsium vulgare*	0.044020306
Cistus salvifolius	0.726722349	*Cistus salvifolius*	0.726722349
Coleostephus myconis	2.037880413	*Coleostephus myconis*	5.337960866
Conyza bilbaoana	0.108772381	*Conyza bilbaoana*	0.05670481
Conyza sumatrensis	0.089370165	*Conyza sumatrensis*	0.044020306
Corrigiola litoralis	0.044020306	*Cytisus striatus*	0.376757405
Cuscuta epithymum	0.036336117	*Dactylis glomerata subsp. lusitanica*	8.80523509
Cynodon dactylon	0.078616438	*Daucus carota*	0.352826273
Cyperus esculentus	16.35993781	*Ditrichia viscosa*	0.044020306
Cytisus striatus	0.376757405	*Echium rosulatum*	1.760812244
Dactylis glomerata subsp. lusitanica	9.616269044	*Erodium moschatum*	0.171615724
Datura stramonium	0.044020306	*Foeniculum vulgare*	0.080356424
Daucus carota	1.209521448	*Fumaria bastardii*	0.068919276

Digitaria sanguinalis	5.499299161	*Fumaria muralis*	0.201063207
Ditrichia viscosa	0.044020306	*Galactites tomentosa*	0.433945318
Echinochloa crus-galli	1.194559694	*Geranium dissectum*	0.43767868
Echium rosulatum	0.440203061	*Geranium molle*	0.041547093
Erodium moschatum	0.171615724	*Geranium purpureum*	0.490206218
Fallopia convolvulus	0.041547093	*Holcus lanatus*	4.239561991
Foeniculum vulgare	0.036336117	*Hypochoeris radicata*	0.271709949
Fumaria bastardii	0.034323145	*Lactuca sativa*	0.182452191
Fumaria muralis	0.242872944	*Lamium purpureum*	0.036608288
Galactites tomentosa	0.348652811	*Leontodon taraxacoides*	0.045349859
Galinsoga ciliata	0.02972673	*Lolium multiflorum*	4.883312902
Galinsoga parviflora	1.383696118	*Lotus pedunculatus*	0.427836996
Geranium molle	0.253085324	*Lythrum junceum*	0.044020306
Geranium purpureum	0.099758639	*Medicago polymorpha*	0.044020306
Holcus lanatus	2.66176533	*Montia fontana s.l.*	2.423411232
Hypochoeris radicata	0.135059148	*Oenanthe crocata*	1.181193674
Lamium amplexicaule	0.07120442	*Ornithopus compressus*	0.041547093
Lotus hispidus	0.830941862	*Parietaria judaica*	0.03767574
Lotus pedunculatus	0.063967679	*Picris echioides*	0.044020306
Lythrum junceum	0.063967679	*Plantago lanceolata*	2.734517583
Medicago lupulina	0.044020306	*Plantago major*	0.044020306
Medicago polymorpha	0.22010153	*Poa annua*	4.416985015
Misopates orontium	0.123503607	*Pseudoarrhenatherum longifolium*	0.036336117
Montia fontana	0.121170562	*Pseudognaphalium luteo-album*	0.05670481
Oenanthe crocata	0.319838396	*Ranunculus muricatus*	0.07120442
Ornithopus perpusillus	0.041547093	*Raphanus raphanistrum*	0.030539703
Paspalum dilatatum	0.226749294	*Rubus ulmifolius*	8.121249491
Phytolacca heterotepala	0.012684504	*Rumex acetosella subsp. angiocarpus*	0.030539703
Picris echioides	0.044020306	*Rumex conglomeratus*	0.078343451
Plantago lanceolata	3.165487806	*Rumex obtusifolius*	0.098563811
Plantago major	0.22010153	*Scrophularia scorodonia*	0.044020306
Poa annua	4.197613718	*Senecio sylvaticus*	0.049020622
Polygonum aviculare	0.037728269	*Senecio vulgaris*	0.07994599
Polygonum persicaria	0.037728269	*Silene gallica*	0.036336117
Pseudognaphalium luteo-album	0.05670481	*Silene latifolia*	0.477878801
Raphanus raphanistrum	0.128830527	*Solanum chenopodioides*	0.044020306
Rubus ulmifolius	8.733454758	*Solanum nigrum*	0.080356424
Rumex acetosella subsp. angiocarpus	0.030539703	*Solanum tuberosum*	0.182452191
Rumex obtusifolius	0.441795258	*Sonchus oleraceus*	0.14954787
Senecio vulgaris	0.512608024	*Spergula arvensis*	0.800131349
Setaria pumila	0.044020306	*Stachys arvensis*	0.237451853
Silene latifolia	0.044020306	*Stellaria media*	0.036336117
Solanum chenopodioides	0.078343451	*Symphyotrichum subulatum var. squamatum*	0.154995634
Solanum nigrum	0.466661568	*Teesdalia nudicaulis*	0.036336117
Solanum tuberosum	1.129309275	*Ulex europaeus subsp. latebracteatus*	3.979003682

Sonchus oleraceus	1.649251477	*Urtica membranacea*	0.03767574
Spergula arvensis	3.376229666	*Vesbascum simplex*	0.044020306
Stachys arvensis	0.634224673	*Vesbascum virgatum*	0.044020306
Stellaria media	0.852354873	*Vicia disperma*	0.207735466
Symphyotrichum subulatum var. squamatum	0.076652184	*Vicia sativa*	0.139314805
Trifolium repens	0.207735466		
Ulex europaeus subsp. latebracteatus	3.979003682		
Urtica urens	0.02972673		
Vesbascum simplex	0.044020306		
Vicia angustifolia	0.978697218		
Vicia hirsuta	0.041547093		
Vicia sativa	0.080356424		
Zea mays	0.605852808		